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REVIEW ARTICLE

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Modelling approaches for mixed forests dynamics prognosis. Research gaps and opportunities

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Abstract

Aim of study: Modelling of forest growth and dynamics has focused mainly on pure stands. Mixed-forest management lacks systematic procedures to forecast the impact of silvicultural actions. The main objective of the present work is to review current knowledge and forest model developments that can be applied to mixed forests.

Material and methods: Primary research literature was reviewed to determine the state of the art for modelling tree species mixtures, focusing mainly on temperate forests.

Main results: The essential principles for predicting stand growth in mixed forests were identified. Forest model applicability in mixtures was analysed. Input data, main model components, output and viewers were presented. Finally, model evaluation procedures and some of the main model platforms were described.

Research highlights: Responses to environmental changes and management activities in mixed forests can differ from pure stands. For greater insight into mixed-forest dynamics and ecology, forest scientists and practitioners need new theoretical frameworks, different approaches and innovative solutions for sustainable forest management in the context of environmental and social changes.

Additional keywords: dynamics, ecology, growth, yield, empirical, classification.

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Introduction

Forests are complex, open, long-term systems with fuzzy boundaries and key elements that change over time. Disturbances influence forests intensively, adding complexity to their dynamics. Models allow scientists to analyse and interpret complex, non-linear systems (Sverdrup & Stjernquist, 2002), but modelling forest dynamics presents several challenges. To fully understand forest dynamics, especially in mixed forests, we need models that incorporate essential aspects such as emergent properties, multiple and multi-scale interactions or spatial, functional and structural variability. The vast amount of very detailed information currently available about forests does not necessarily provide a better understanding of ecosystem structure and functioning as a whole (Fabrika & Pretzsch, 2013).

Several silvicultural foundations, such as site productivity, stability or tree growth allocation (between species and at individual level) are challenged by global change but remain unknown for mixed forests. For example, recent works on yield distribution have shown that species interactions in mixtures generate emergent properties and modify the stand environment, function and structure (Pretzsch *et al.*, 2015). Along with risk assessment, mixed-forest modelling should generate flexible outputs for different ecosystem services provided by different mixtures.

Models can provide useful information for operational forestry but the information needed by forest managers depends on management intensity and the ecosystem services being managed. In their current form, less than one-third of the existing forest growth models consider mixing effects or can be used to predict growth in mixed-species stands (Pretzsch *et al.*, 2015).

From an operational perspective, models need to be developed for use in an entire portfolio of silvicultural strategies, including sustainability criteria and indicators. Thus, the participation of many types of end-users is a key element for analysing complex systems with diverse values. Information and models to identify sustainable, multifunctional forest management options are needed for mixed forests especially (Hasenauer, 2006; Rennolls *et al.*, 2007; Mendoza & Vanclay, 2008). To be useful for operational forestry, models should be clearly specified, tested for prediction accuracy, embedded in management procedures and provide easily understandable results, well-documented processes and user-friendly interface (Teufel *et al.*, 2006). Clear objectives defined by the relevant stakeholders (owners, managers, general public…) should precede any silvicultural treatment of forest stands. In even-aged monocultures, applying proper silvicultural procedure(s) to achieve stated objectives is much easier than in closer-to-nature, complex, multi-species stands. A new generation of relevant models for mixed forests is needed to address important issues such as: (1) the conditions for successful natural regeneration (natural succession) in multi-species stands (Schütz, 1999; Diaci, 2006; Bauhus *et al.*, 2013); (2) the growth dynamics of coexisting tree species in a given mixed stand compared to their monocultures; (3) how neighbouring species affect silvicultural treatments (cleaning, tending, thinning, regeneration cutting) and overall forest stability; (4) the natural tree mortality rate in mixed stands and how it can influence the remaining trees; (5) the probabilities of natural disturbances occurring in mixed-stands; (6) below-ground processes and relationships between root systems of various tree species (Rothe & Binkley, 2001; Schmid & Kazda, 2001, 2002; Shanin *et al.*, 2015), along with their impact on above-ground species performance; (7) converting single-species stands to multi-species stands and the requirements of all tree species in the future stand composition (Kenk & Guehne, 2001; O'Hara, 2001) and (8) the ecosystem services provided and the trade-offs between them under different silvicultural conditions.

Forest ecosystems stretch from the atmosphere to the lowest layers of the soil. Therefore, forest systems are very complex and diversified, with many factors and interactions that affect stand dynamics. Models transfer the complexity and interactions of multiple forest components into a comprehensible structure that can then be refined, step by step. A model integrates the modeller's knowledge and understanding of the system to (1) test overall understanding of a system and (2) predict future forest development or deduce past evolution.

The modelling concept (Kurth, 1994) classifies models as empirical, process-based and structural. They can be further classified according to temporal-hierarchical level (Pretzsch, 2001), hierarchical-spatial level (Lischke, 2001), and other parameters (Munro, 1974; Shugart, 1984; Vanclay, 1994; Houllier, 1995; Liu & Ashton, 1998; Franc *et al.*, 2000; Porte & Bartelink, 2002; Pretzsch *et al.*, 2008). Based on the (i) modelling object, (ii) spatial resolution, (iii) temporal resolution and (iv) concepts to be applied, ten model categories can be defined (Lischke, 2001 modified by Fabrika & Pretzsch, 2013 and Fabrika *et al.*, 2018): (a) eco-physiological tree models (Hauhs *et al.*, 1995), (b) functional-structural plant models (Prusinkiewicz & Lindenmayer, 1990), (c) big leaf models (Landsberg & Waring, 1997), (d) empirical distance-dependent tree models (Ek & Monserud, 1974), (e) empirical distance-independent tree models (Wykoff *et al.*, 1982), (f) tree gap models (Botkin *et al.*, 1972), (g) cohort gap models (Bugmann, 1996), (h) distribution models (Clutter, 1963), (i) stand models (Assmann & Franz, 1965) and (j) biome models (Holdridge, 1947).

As a major driver of forest resource availability, forest productivity remains a fundamental concern in forestry. In practice, low-cost operational tools for predicting forest site productivity are needed to inform tree species selection, optimal silvicultural guidelines and timber yield forecasts for local to regional forest planning. From the first simple yield tables compiled from past empirical data, we have advanced to develop individual tree growth models that handle competition between trees and crowns in even-aged, uneven-aged and mixed stands. They also incorporate emergent properties (such as self-thinning or optimum basal area) and complex interactions (such as over or under-yielding). Currently, mechanistic, process-based models are being developed to better address mixed-species stand dynamics and the impact of environmental changes on forest growth. With climate change comes increased uncertainty. Models that cover a range of possible developments provide usable information for forest management planning and decision-making. Furthermore, despite the importance of non-timber forest products and services, forest management and planning methods and models in Europe have traditionally been oriented towards wood production. Consequently, foresters lack models for multifuncional managed forests or for optimizing management to address demands other than wood production. All these different needs promote hybridisation of modelling approaches, especially process-based, empirical and eco-physiological models, and lead to serialized use of downscaling or upscaling procedures. Downscaling involves shifts in comparison of the initial scale (closer to single individual level) towards finer resolution in space and shorter time intervals. Upscaling moves from shorter to longer time intervals, from finer to coarser spatial units and from single cell or organs to the community level.

The objectives of this review are to: 1) revisit approaches to modelling mixed-species dynamics, 2) assess the data requirements and data sources needed to parametrize existing models, 3) review the mixed-forest modelling components, 4) identify model evaluation methods, and 5) review existing models and model platforms in Europe. This review complements and expands that of Pretzsch *et al.*, (2015) by including model classification based on the respective modelling concept, a discussion about the suitability of different modelling approaches for mixed forests and a description of different model platforms that can provide greater insight regarding mixed stand ecology and dynamics as well as the development of management prescriptions.

Approaches to predicting mixed forest growth

Forecasting mixed forest development is much more complex than for pure stands, due to the need to express interspecific interactions resulting from the resource demands, space filling requirements and growth patterns of the different tree species involved in the mixture. Mixed stands are often more structurally complex than pure stands (Pretzsch *et al.*, 2016) and may create more vertically structured forests based on the varying growth rates of individual tree species. Thus, mixed forests generally use stand space (both horizontally and vertically) better than pure stands. Pretzsch (2009) has shown that in mixed stands, basal area development significantly deviates from the Assmann theory (Assmann, 1961), depending on stand density, and that incremental interactions depend on species proportions in mixed tree species (Pretzsch *et al.*, 2010, 2013). From a methodological point of view, the best way to model mixed-stand development is to take the complex 3D space into account (horizontally and vertically) and include species identity and size as drivers along with stand productivity. Among the many approaches to identifying the effects of species composition on stand growth, forest modellers usually rely on four: (i) averaging pure stand characteristics, (ii) introducing multipliers to look at mixing effects, (iii) introducing competition measurements that include species identity or (iv) using an eco-physiological approach (Pretzsch *et al.*, 2015).

Weighted average of pure stand features

When no information is available for mixed-forest growth, stand development is simply assumed to follow the weighted average of pure stands. Appropriate pure stand models should thus be selected for each species in the mixture, along with suitable site indices and equations for thinning effects. The outcomes from the pure stand models (i.e., growth and yield characteristics, stand density) are weighted by mixing the proportions to obtain an average of the expected performance of mixed forests. However, this approach does not consider possible species interactions in the mixture, and thus cannot properly account for real growth competition or facilitation. Wiedemann (1942) used this approach to develop yield tables for mixed stands of Norway spruce and European beech.

Using multipliers to consider mixing effects

By comparing pure-stand model forecasts with mixed-stand permanent plot data (fine-tuned with data from close permanent pure stand plots), mixing effects can be assessed as multipliers ($Y = m * \hat{Y}$). As the growth and yield characteristics of forest monocultures are well known at both stand and tree level, the multiplier (m) represents the deviation of specific species response in mixed stands compared to pure stands. This approach has been applied for quantifying the growth response to different environmental conditions such as site fertility, insect attacks or fertilization (Wykoff *et al.*, 1982; Monserud & Sterba, 1996; Komarov *et al.*, 2003). However, the underlying processes remain largely unknown.

Including competition indices in the model

When the availability of growing space is included in growth models, the 2D or 3D forest structure and the competitive status of the individual trees can be quantified using competition indices (CI). CI help to adjust growth and mortality probability for the given projection period. As stand structure and tree growth are linked to CI, mixing effects could lead to significant deviance in stand development forecasts.

To integrate the different effects of the species on the mixture, distance-dependent or species identity CI can be used to look at: (i) the specific differential response of species to growing area requirements and (2) the response of each species to competition for above- and below-ground resources. Models by Södeberg (1986), Hasenauer (1994), Köhler & Huth (1998), Hynynet *et al.* (2002), Pretzsch (2002), Hynynen & Ojansuu (2003) Pukkala *et al.* (2009) , or Elfving (2011a and 2011b) are examples of this approach.

Eco-physiological process approach

A different approach is to directly consider the actual resource partitioning between species in the mixture. Here, competition for resources is simulated for each individual tree or cohort and the species-mixing impact is assessed through feedback between species-specific spatial structures and tree growth as well as between a tree's individual environment (resource availability) and its dynamics (growth, survival probability, …). Species mixing modifies resource distribution (light, water, nutrients) and uptake within the stand, which can have a huge impact on growth rates at tree and stand level. Models based on this approach have been developed for different forest types and mixtures (Kimmins *et al.*, 1990a, 1990b, 1999; Kellomäki & Vaisanen, 1997; Grote & Pretzsch, 2002; Rötzer *et al.*, 2009). The eco-physiological approach to modelling mixed stands can be applied using big leaf models, frequency-based stand models and population (species) stand models. When no information about eco-physiological processes in mixed stands is available, the first two approaches (weighted average and multipliers) can be used to adjust known eco-physiological responses from pure stands. However, eco-physiological tree properties that emerge in mixed but not mono-specific stands are neglected.

Input data for simulating mixed forests using forest growth models

Mixed-forest modelling requires more input data because it deals with more complex objects; as modelling detail increases, input data also increases. Input data requirements vary according to the modelling approach used. Empirical models require biometric parameters of trees or stands and/or a generalized site description (based on site classification or other parameters) as input. Process-based models require inputs that are directly linked to eco-physiological and ecosystem processes.

The model category also affects the type of input data. At the community level, for example, species composition, stand density, and tree species properties (mean diameter, mean height, basal area or volume) are required, while tree diameter, tree height and crown properties are required at the organism level. For distance-dependent models, tree positions in the stand are also needed. This is true for both empirical and process-based models. For the latter, additional data are required: leaf area index and total biomass per species for models at the population level and leaf area of single trees, biomass of individual tree parts, and spatial distribution (2D or 3D) for models at the organism level.

Several tools have been developed to generate different types of input data, including reconstruction of stand structure (Brandtberg, 1999; Surový *et al.*, 2004; Klemmt & Tauber, 2008) and reproduction (Pommerening, 1999; Pommerening *et al.*, 2000), structure generators (Pretzsch, 1993; Nagel & Biging, 1995; Merganič & Sterba, 2006), site generators (Kahn, 1994; Fabrika, 2005), weather generators such as WGEN, (Richardson & Wright, 1984), SIMMETEO (Geng *et al.*, 1986, 1988), TAMSIM (McCaskill, 1990), CLIMGEN (Clemence, 1997), MET&ROLL (Dubrovský, 1997), LARS-WG (Semenov *et al.*, 1998), AAFC-WG (Hayhoe, 2000), MARKSIM (Jones & Thornton, 2000), RUNEOLE (Adelard *et al.*, 2000), WM2 (Hansen & Mavromatis, 2001) or CLIMA (Donatelli *et al.*, 2009) and numerical weather prediction models such as ALADIN (Huth *et al.*, 2003). Models that account for horizontal and vertical stand structure are more suitable for mixed stands, because they capture data on interactions among trees. Thus, tools for structure reconstruction, reproduction and generation are particularly useful for modelling mixed-species stands.

Components of growth models

Modelling for forest ecosystem management (including mixed-forest modelling) should integrate different scales (temporal and spatial) and various disciplines for balanced prediction of different forest ecosystem services (Pretzsch *et al.*, 2008). As already mentioned, mixed forests present distinct features (self-thinning, allometry, etc.), so data from pure stands must be evaluated before it is transferred. However, model components from pure stands may serve as starting points for modelling different aspects of mixed-stand forest development (mortality, competition, growth, nutrient cycle, thinning interventions, felling approaches or regeneration establishment).

As an example, competition indices with modified coefficients that depend on the species or group of species to which some competitors belong to can be used. Indices based on the vertical light cone method (Pukkala & Koloström, 1987; Pukkala, 1989; Biging & Dobbertin, 1992; Pretzsch, 1995) are particularly suitable for calculating the competitive pressure of individual competitors on the subject tree. Significant improvements can be achieved when the interactions of different tree species are considered in tree increment values. In the SILVA model (Biber *et al.*, 2013), for instance, the mixing effect is included as a multiplier.

Thinning interventions are one of the most important and common silvicultural treatments in forestry. Their integration into forest models is crucial because they shape forest structure (Schall *et al.* 2018). Once a thinning intervention is defined (type, selection criteria, intensity, rotation) it should not be difficult to simulate; the model only requires the definition of the trees to be removed from the stand. However, thinning alters stand structure, environment (microclimate, nutrient cycle, etc.) and dynamics (growth and mortality). Therefore, it is necessary to consider both thinning algorithms and thinning response functions.

Algorithms for modelling thinning interventions based on different tree selection criteria, including tree species, are already well described (Fabrika & Ďurský, 2005; Fabrika & Pretzsch, 2013). At stand and size frequency levels, thinning intervention simulations require control functions to predict changes in stand structure for a given thinning rule (Bravo-Oviedo *et al.*, 2004; Mora *et al.*, 2012). Simulating thinning operations in mixed forests is challenging because the results of a given thinning rule are generally expressed in a simplified way and may vary drastically from actual dynamics in complex forests (Söderbergh & Ledermann, 2003). Thus, real data from different thinning schedules and species proportions for a given mixture would be needed to effectively parametrize control functions. Lack of adequate thinning indices for mixed stands, particularly for aspects related to species composition, presents another difficulty (del Río *et al.*, 2016).

Many empirical distance-dependent tree models might inherently predict tree response to thinning from the change in stand structure, whereas population stand models usually require insertion of thinning response functions (Weiskittel *et al.*, 2011). Generally, thinning response is considered in forest models with modifiers reflecting the thinning type, timing, and intensity in the main driver functions of the model. Changes in species proportion would also be required for mixed stand models.

Besides timber production and economic criteria in simulations of forest growth and dynamics (expressed through volume growth, basal area, assortment classes, net present value-NPV, etc.) (Mäkelä *et al.*, 2000; Lindner *et al.*, 2002; Rollin *et al.*, 2005; Pukkala, 2015), there is increasing demand for model predictions that address issues such as biodiversity (Purves & Pacala, 2008; Vilà *et al.*, 2013; Forrester & Tang, 2015; Lafond *et al.*, 2015; Reyer *et al.*, 2015), carbon fluxes and sequestration (Backéus *et al.*, 2005; Schmid *et al.*, 2006; Bravo *et al.*, 2008; Seidl *et al.*, 2008; Schwenk *et al.*, 2012; Collalti *et al.*, 2014; Fischer *et al.*, 2014; Mika & Keeton, 2015; Borys *et al.*, 2016), water yield (Cademus *et al.*, 2014), groundwater recharge (Fürstenau *et al.*, 2007) and albedo-related radiative forcing (Lutz *et al.*, 2016). This information is needed to better understand trade-offs among forest ecosystem services in multifunctional approaches for sustainable forest management (Mäkelä *et al.*, 2012).

Density-dependent mortality is an essential component of forest dynamics. As with other model components, there are more detailed models for pure stands than for mixed-species forests. Mortality or survival are usually modelled using a logistic function to estimate the probability that a tree will die or survive after a certain period of time, depending on the event measured. Mixed-forest approaches include separate modelling of individual tree mortality/survival for each species (Temesgen & Mitchell, 2005, Weiskittel *et al.*, 2016) or modelling the response of groups of species according to similar functional characteristics, such as growth rate or shade tolerance (Zhao *et al.*, 2004). Upscaling from individual tree to stand-level mortality has been indicated as an important issue that is dependent on data quality (Monserud *et al.*, 2005). For mixed-species forests, species-specific mortality functions or the species-specific threshold in the logistic model can be used as expansion factors for upscaling (Weikittel *et al.*, 2016).

Forest growth and yield models depend on the relationship between dendrometric variables such as height and crown attributes related to diameter at breast height, under the assumption of constant allometry. However, intra- and interspecific variability of allometric coefficients is common in trees (Duursma *et al.* 2010), leading to intra- and inter-competition effects that might be related to stress tolerance and functional traits, such as shade tolerance and wood density (del Río *et al.*, 2019, Forrester *et al.*, 2018, Ducey, 2012).

Evaluation of forest models

For mixed and pure forests alike, growth model performance must first be evaluated in terms of biological interpretation and logical behaviour, according to the current knowledge of the system. Model evaluation is rather context-dependent and relative (Shifley *et al.*, 2017); the complex and biological consistency of models for mixed-stand dynamics should reflect individual tree behaviour for component species and stand-level responses that frequently are not the simple aggregation of individual trajectories. Precision and accuracy must be tested against independent data, adding another important caveat to the evaluation process: stand conditions, including species composition and proportions can vary greatly in space and time. In situations where true independent data is lacking or benchmark values are scarce, re-sampling techniques such as cross-validation, jack-knife techniques and boot-strapping are preferred (Vanclay & Skovsgaard, 1997). Soares *et al.* (1995) identified five steps for evaluating forest models: (1) theoretical and biological assessment, (2) analyses of statistical properties, (3) characterization of errors, (4) bias and precision testing and (5) sensitivity analyses of model parameters. Sensitivity analyses study how the output variation of a model can be qualitatively or quantitatively apportioned to different sources of variation (Saltelli *et al.*, 2008).

Quantifying uncertainty in forest resource projections is a complex challenge and very important in forest management and decision-making. (Schadauer *et al.* 2017). There are a few studies on the precision of growth predictions (Gertner & Dzialowy 1984, Mowrer and Frayer 1986, Gertner 1987, Mowrer 1991, Kangas 1997, Saltelli *et al.*, 2008; Fortin *et al.*, 2009;), but uncertainty in model projections is still not generally addressed. Though single-tree-based models have proven particularly suitable for mixed-stand simulations and have gained popularity, forest management decisions are usually made at stand level. Error propagation from tree to stand level, as well as uncertainty quantification are ignored (Zhang *et al.*, 1997). The different sub-models that build up single-tree-based models also contribute to error sources (Kangas, 1999) and uncertainty, which tends to increase with projection length as prediction errors from prior periods accumulate (Kangas, 1997). Uncertainties are even higher in models conceived for complex forests, due to mixing effects like overyielding and inter-specific interactions that are absent in mono-specific, even-aged stands (Pretzsch *et al.*, 2015). To tackle the uncertainty problem, estimators based on likelihood or pseudo-likelihood functions have been used (see Schadauer *et al.* (2017) for more details). These can be combined with Monte Carlo approaches to assess the uncertainty related to the stochasticity of the processes (Fortin *et al.*, 2009). This might work under the assumptions that the model limitations are used deterministically, that inputs have zero variance and that the outputs are unique. The evaluation process is then completed with an uncertainty analysis to quantify the overall uncertainty associated with the response as a result of uncertainties in the model input (Saltelli *et al.*, 2008). Uncertainty in forest model outputs has also been assessed using Bayesian synthesis or melding (McFarlane *et al.* 2000), Bayesian averaging (BA) and model comparison (BMC) for outputs from several models (van Oijen *et al.*, 2013, Londsdale *et al.*, 2015). However, these approaches have been applied to single species and the accountability of uncertainty associated with parameters from multiple-species stands is still challenging.

Application of forest models and model platforms for mixed forests: some examples from Europe

In European forest ecosystem management, integration of different forest functions is a characteristic concept (Resolution H1 MCPFE in Helsinki 1993; Pretzsch *et al.*, 2008; Ammer & Puettmann 2009). Heterogeneous, uneven, mixed-species forest stands are currently advancing in Europe (Bravo-Oviedo *et al.*, 2014), as they indisputably fulfil many ecological and social functions and services better than even-aged monocultures (Gamfeldt *et al.*, 2013). However, management of structurally complex mixed forests is no easy task in practice (Coll *et al.*, 2018). Using models for mixed forests and their outputs can support management and pave the way for better understanding of the underlying processes at the organ, individual tree and ecosystem levels. Such models should be widely utilized in the education system and in training activities for students and forest managers. Simulation and analysis of thinning regimes by means of models provides an excellent educational tool for mixed forest tending operations during silvicultural courses. For instance, different types of thinning can be simulated by diverse model algorithms that mimic thinning from below, from above, by single tree selection, by target diameter or geometric thinning (Söderbergh & Ledermann, 2003). Many models also allow users to interactively perform different types of thinning (Seifert, 1998; Fabrika, 2003). Results in the form of tables, charts, and 3D visualization enable the comparison of the effects of different thinning regimes on structure, stability and productivity for a given mixed stand. This 'thinning training tool' can also be applied to marteloscope experiments (Poore, 2011), to test and demonstrate the impact of the thinning performed by each trainee, using 3D visualisation and other graph and table outputs. To this end, many existing empirical models and simulators can be used, such as SILVA (Pretzsch, 2002), SIBYLA (Fabrika & Ďurský, 2005), BWINPro (Nagel & Schmidt, 2006) or IBERO (Bravo *et al.*, 2012). Process-based models such as FORLAS (Brzeziecki, 1999; Zajączkowski, 2006) can also serve as an educational tool during forest ecology courses and promote better understanding of natural forest secondary succession processes, under current climate parameters and for different climate change scenarios. Though mixed-forest models are gaining popularity in many European university courses (Pretzsch, 2009; Fabrika & Pretzsch, 2013), greater use of available models in forest practice is still lacking. In the following paragraphs, we provide a short description of several models that are frequently used in Europe for modelling mixed stands, based on different approaches (hybrid, process-based, empirical) and resolutions (landscape, stand and individual tree level).

SIBYLA

SIBYLA is a hybrid model containing empirical, process-based and structural modelling principles (Fabrika, 2007). The core of SYBILA is a spatially explicit (distance-dependent) empirical tree model that requires input data for individual trees (position, diameter, height, crown parameters, quality parameters). If the data are not available, a forest structure generator is used. The given or generated forest structure is displayed as a 3D forest structure model. From tree parameters and spatial structure, the calculation model computes all the important outputs for production, biomass, biodiversity, revenues and costs. Forest development is simulated in 1-year time-steps using mortality, disturbance, thinning, competition and increment models, as well as a model of forest regeneration. It is directly parametrised for 5 basic tree species: common beech, pedunculate or Sessile oak, Norway spruce, silver fir, and Scots pine. In total, 26 different tree species can be simulated, but some of them are derived by modifying the growth processes of the 5 basic tree species. The mortality model focuses on intrinsic and growth-dependent mortality (Fabrika, 2007). The disturbance model addresses induced tree mortality caused by external disturbance factors. It is based on modelling risk and incorporates the probabilities of hazard, exposure and vulnerability for different disturbance agents: wind, snow, ice, bark beetles, timber borers, defoliators, wood-destroying fungi, air pollutants, drought, fire and illegal cutting (Fabrika & Vaculčiak, 2009). Different types of thinning can be simulated: from below, from above, neutral thinning, target trees method, target dimensions method, target frequency distribution method, geometric method, and interactive thinning (Fabrika & Ďurský, 2005). The competition model is based on the crown light competition index (KKL) proposed by Pretzsch (1995). The age-independent increment model simulates tree diameter and height increments based on the reduction of their growth potential. Growth potential is defined according to the ecological site classification proposed by Kahn (1994), based on climate and soil characteristics, and modified to reflect the competition pressure of trees and tree vitality, as determined by tree crown size. If tree age is unknown, it is derived from the growth potential and the current tree height at the beginning of the growth period. The regeneration model is an ingrowth model that generates new tree generation in a forest stand (Merganič & Fabrika, 2011). This model is composed of individual-tree generator sub-models along with a diameter and height distribution model for the new generation and a sub-model for locating regeneration in the stand.

SILVA

SILVA (Pretzsch *et al.*, 2002) is a single-tree-based, position-dependent simulation model designed for operating at the stand or large-area (landscape) level. It includes the most important tree species and site conditions in Central Europe. The model can handle different input data resolutions. The minimum input information required at stand level is the quadratic mean diameter and number of trees per hectare for each species in the stand. Maximum input consists of a list providing diameter at breast height (dbh), height, height to crown base, crown diameter, and position for each tree. The site information needed is restricted to a minimal set of climatic and soil variables that are usually available to practitioners. For large-area simulations, the SILVA interface handles grid-based forest inventory data, which it uses to simulate landscape-level scenarios in one run. SILVA growth functions describe the growth reaction of each tree, according to given size and site conditions, and the competition exerted by its neighbors. All SILVA functions exclude stand or tree age as an explanatory variable, so the model is not restricted to even-aged pure stands. SILVA can simulate a broad range of treatments, from traditional thinning from below to selective thinning to target-diameter felling. Different types and intensities of thinning interventions or final harvests can be applied at stand and landscape levels in one simulation run. Model output is designed for multi-criteria scenario assessment, covering classic growth and yield information as well as financial parameters and indicators for forest structure and diversity. Special landscape-level constraints such as habitat or protection areas can be considered by stratifying the inventory data accordingly and defining specific treatments for strata with constraints. SILVA does not command an automatic optimization algorithm. Optima are usually approximated manually by sensibly defining and modifying scenario settings.

BALANCE - a process based, spatially explicit forest growth model

The process-based growth model known as BALANCE (Grote & Pretzsch, 2002) calculates the three-dimensional development of trees or forest stands and estimates the consequences of environmental impacts. As an individual tree model, BALANCE simulates growth responses at tree level, which enables estimation of the influence of competition, stand structure, species mixture, and management impacts. Tree development is described as a response to individual environmental conditions, as these change with the development of each individual tree. The individual carbon, water and nutrient balances of European beech, Sessile and common oak, Norway spruce, Scots pine and Douglas fir are the fundamental processes for the growth simulations. Micro-climate and water balance are calculated for each segment of each layer using temperature, radiation, precipitation, humidity and wind speed measurements from climate stations. While these calculations are computed daily, the physiological processes of assimilation, respiration, nutrient uptake, growth, senescence and allocation are calculated in 10-day time steps from the aggregated driving variables. In this way, CO_2-concentration, soil condition, competition between individuals and stress factors such as air pollution and nutrition deficiency can be considered in addition to the weather conditions when modelling tree growth. BALANCE includes different approaches for estimating the environmental conditions for each individual tree. To depict relationships between environmental influences and growth, the annual foliage development cycle must be known beforehand. Allocation of carbon and nitrogen to roots, branches, foliage and stem is computed according to functional balance and pipe model principles.

LandClim

LandClim (Schumacher et al, 2004 and 2006) is a stochastic forest landscape model designed to study spatially explicit forest dynamics at the landscape scale over long time periods and with fine spatial resolution (25 m x 25 m grid cells). This model uses a cohort approach in which trees of the same age and species are simulated by one representative individual. So far, thirty-eight of the most common tree species from Central Europe and the Mediterranean region have been parametrized. Tree cohorts compete with each other for light and water, creating changes in species mixtures along environmental gradients. In water-limited conditions, the drought tolerance of each species determines growth and relative competitive strength, which influences the species mixture that evolves. With increasing altitude and latitude, temperature becomes a limiting factor and tree growth is controlled by species-specific minimum growing degree-day requirements. Trees also compete for light, which is determined by the vertical structure, canopy characteristics and species-specific shade tolerances and foliage types. Shade intolerant species dominate in early successional stands and are gradually outcompeted by more shade tolerant species as the canopy closes. LandClim has been used to simulate potential natural vegetation as well as managed forests, by simulating interventions such as harvesting, thinning and planting. The model can also simulate the impact of disturbances, including fire, windthrow and bark beetle outbreaks, on forest dynamics.

SORTIE-ND

SORTIE-ND (Canham *et al.*, 2005) is an individual-based model of forest dynamics that records the specific location of each tree within a plot and simulates recruitment, growth, and mortality for individual trees. At a given time, the model state is defined by a plot, trees and grids. The plot where the model runs is characterized by a size, a climate and a geographical location. The trees are defined according to species, life history stage (seedlings, saplings, adults…), size and position in the plot. Finally, the grids cover the entire plot and provide information about variation in the variables throughout the space (soil fertility, light availability at the forest floor, etc.). In SORTIE-ND, the change of the model state at a given time step is driven by a number of behaviours that are selected and parameterized by the user. Most important behaviours rely on the computation of resource availability, tree recruitment and growth and mortality processes in seedlings, saplings and adults.

The spatially explicit nature of the SORTIE-ND model makes it especially suitable for simulating mixed-forest dynamics. It has successfully simulated fine-scale spatial processes such as neighbourhood competition for resources (Canham *et al.*, 2004, 2006), seed dispersal and recruitment patterns (Ribbens *et al.*, 1994; Papaik & Canham, 2006), and the effects of different natural or anthropogenic disturbances such as windthrow, silvicultural treatments and insect outbreaks (Canham *et al.*, 2001; LeGuerrier *et al.*, 2003; Uriarte *et al.*, 2005; Beaudet *et al.*, 2011; Ameztegui *et al.*, 2017).

SORTIE-ND was recently used at the European level to evaluate the effects of climate change on conifers in mixed-forest dynamics in the montane-subalpine ecotone of the Pyrenees (Ameztegui *et al.*, 2015). These forest areas are mostly composed of two shade-intolerant pines (*Pinus sylvestris* L. and *Pinus uncinata* Ram.) and a shade-tolerant species (*Abies alba* Mill.). Like many other mountainous transitional areas, they are considered to be particularly sensitive to the predicted increases in temperatures (Ameztegui & Coll, 2011).

CAPSIS

The CAPSIS (Computer-Aided Projection of Strategies In Silviculture) project has been developing in France since 1994, with the main objective of simulating the consequences of silvicultural treatments based on scientific knowledge. It was built to be a perennial, open and dynamic integration platform for forestry growth and yield models (Dufour-Kowalski *et al.*, 2012). A set of rules have been defined to encourage collaborative development, model sharing and code reuse. Every component developed, except the CAPSIS modules (the model implementations), is distributed under a free license (Lesser General Public Licence), so that the core application and all extensions can be used by anyone. CAPSIS can integrate diverse models involving various dynamic processes (growth, competition, mortality, regeneration, dispersion…) and specific properties such as radiative balance, genetic information at the individual level, internal biomechanics or wood quality. The user-friendly graphical interface makes the models accessible to forest managers. A full description of CAPSIS can be found in Dufour-Kowalski *et al.* (2012). The platform characteristics and the support provided to the modellers are crucial to model development. Similarly, the possibility of developing specific modules for coupling mono-specific models makes it possible to adapt generalized original models developed for pure stands and apply them to mixtures. The platform currently offers models for various species in pure and mixed stands. Output results include forest development projections for multi-species mixtures, stand structures and silvicultural regimes; evaluation of mixture effects on basal area growth according to environmental variables; tree growth and resource use in mixed stands; and simulation of multispecies tropical forest dynamics (for a list of the CAPSIS projects, see http://www.inra.fr/capsis/).

sIMfLOR

The sIMfLOR simulators' platform was created to implement different growth models with a common philosophy. It was developed with an easily-updatable, user-friendly scope that is sensitive to forest management and climate change for the main tree species in Portugal. StandsSIM.md Management Driven simulator (Barreiro *et al.*, 2016) was recently developed to overcome the limitations of the existing stand-level simulators in sIMfLOR by covering more tree species, stand structures and stand compositions. StandsSIM.md-MD was programmed in a modular form, linking five main Modules: 1) The *Configuration Module* defines all simulation parameters, namely the type of model to be applied (stand-level, individual-tree or 3PG), the simulation mode, the number of years to simulate and the hard disk locations of input and output files; 2) The *Input Module* is based on a set of inputs that characterize the initial forest condition and structure, depending on the type of growth model; 3) The *Growth Module* includes empirical individual tree and stand growth models and a stand-process-based growth model (only available for eucalyptus at present) to update growth using the selected model for a given tree species, according to a set of forest management prescriptions; 4) the *Management Module* defines the prescriptions that schedule the sequence of Forest Management Approaches, each corresponding to a stand rotation cycle, and their primary silvicultural operations throughout the simulation period; 5) The *Output Module* produces the 'yield-table output', containing one yield table per stand and prescription, with an ample list of stand variables when running in 1-PPS mode (one prescription applied to each stand) or several prescriptions per stand when running in MULTI-PPS mode. In the latter mode, an additional/alternative output file structured to serve as input to a linear programming optimizer can be produced. StandsSIM.md runs tree species separately on 1-year time-steps and the present version does not apply to mixed-species stands. These can be simulated as pure stands with an area corresponding to the proportion of the species basal area in the stand. The resulting mixed-forest forecast is based on weighted pure stands (by area proportion).

Heureka

The Swedish University of Agricultural Sciences (SLU) developed the Heureka decision support system (DSS) (Heureka 2010, www.slu.se/heureka) that is intended for a broad array of users (Lämås & Eriksson, 2003; Wikström *et al.*, 2011). Heureka is the successor of the Hugin forest planning system (Fahlvik *et al.*, 2014) and relies on the empirical growth models being developed in Sweden since the 1980s. Heureka forestDSS is based on a common core of stand and single-tree growth and yield models with an interactive stand simulator. From this, four main software applications have been developed: (1) RegWise analyses (tool for long-term, large-scale areas such as countries, regions) based on National Forest Inventory sample plot data, (2) PlanWise (tool for long- and medium-term planning on small to large forest estates, can be applied to sample stands or all stands on the estate), (3) PlanEval (a tool for MCDA analyses) and (4) StandWise (an interactive stand simulator for analysing management of individual-stand actions and development). In a recent evaluation (Fahlvik *et al.*, 2014), Heureka empirical models (based on historical growth data) were shown to provide sound and credible growth predictions that do not depend upon projection length. Stand-level models presented greater precision than individual-tree models.

The core growth and yield models are based on NFI data, which have been demonstrated (Fridman *et al.*, 2014) as a reliable source of long-term forest state time series for describing and forecasting different ecosystem services. Common mixtures in Sweden are spruce-pine, spruce-birch and pine-birch. More complex and unusual mixtures are difficult to handle in the system. The Heureka system is frequently used in research, education and practical forestry. In 2013, the forestry organisation formalised an agreement with the relevant authorities and industry concerning how to finance the system, enabling its continuous update and renewal.

IBERO

IBERO is an individual-tree, distance-independent growth model (Bravo, 2005) that relies on different modules (1) imputation of missing data (Static equations to input crown, bark thickness, height-diameter...), (2) productivity (site index curves, site productivity discriminant rules…) (3) ingrowth (two-steps' models), (4) mortality functions, (5) estimation of environmental services provision (stem taper equations, link functions for carbon, mushroom yield…) and (6) growth equations (diameter and height projection). Currently, mixtures of *Pinus sylvestris* and *Pinus pinaster* can be simulated with IBERO on the SIMANFOR platform (Bravo *et al.*, 2012), using parametrizations from pure stands that have been integrated for testing and evaluation purposes. Mixed forest forecasts are based on growth of individual trees in pure stands, which are then combined to obtain the mixture effect. A new parametrization for this mixture is being developed from the results of ongoing experimental and monitoring work (Riofrio *et al.*, 2017).

Research gaps and opportunities

Mixed forests are complex systems that differ from pure stands in their response to environmental and management conditions. Tree allometry is also modified when trees grow in mixtures. Thus, the use of equations developed for monospecific stands can lead to erroneous growth estimates. The effect of mixtures can be included in models as a modifier (i.e., considering species proportion in different ways) or as a differential competition factor in growth and mortality equations. Studies analysing changes in allometry are observational, and understanding of the mechanisms behind such changes is significantly lacking. Species interaction, along with inter- and intraspecific competition during density-dependent mortality events, also need further research, as many models are still based on weighted averaging. Additionally, mixed forest structure can be even-aged or uneven-aged and single- or multi-storeyed. This makes forecasting dynamics far more complicate and requires updated theoretical frameworks.

The information needed by forest managers depends first on whether forests are being managed primarily as wood production systems or – at least partially – for other forest ecosystem services as well. Second, it is important to know whether the managers are closely involved with operational decisions or more concerned with forest policy issues and longer-term considerations, including the sustainability of various options. For forest practice, in the field of forest planning and multicriterial decision analysis (MCDA) support systems, some important attributes should be considered, including clear specification of purpose and documentation of model limits, reasonable accuracy, user-friendly handling and ways of communicating the results (Teufel *et al.*, 2006). Visualization of model results is probably one of the more important tools for communicating results, and internet-based knowledge systems (e.g. smart-phone applications) need to be developed to reach many forest owners (Hannertz *et al.*, 2010). Until now, universities and research institutes have generally developed these models and systems. To ensure greater practical implementation in the future, closer cooperation between end-users and developers is needed. This requires better understanding of models and systems by forest practitioners, and constant communication between model developers and practitioners, which will benefit both groups. Because future models and systems should developed for use in an entire portfolio of silvicultural strategies, including sustainability criteria and indicators, end-user participation is a key element for analyzing complex systems with diverse values.

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